Research Article

Dynamics of Newly Established Elk Populations

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ABSTRACT The dynamics of newly established elk (*Cervus elaphus*) populations can provide insights about maximum sustainable rates of reproduction, survival, and increase. However, data used to estimate rates of increase typically have been limited to counts and rarely have included complementary estimates of vital rates. Complexities of population dynamics cannot be understood without considering population processes as well as population states. We estimated pregnancy rates, survival rates, age ratios, and sex ratios for reintroduced elk at Theodore Roosevelt National Park, North Dakota, USA; combined vital rates in a population projection model; and compared model projections with observed elk numbers and population ratios. Pregnancy rates in January (early in the second trimester of pregnancy) averaged 54.1% (SE = 5.4%) for subadults and 91.0% (SE = 1.7%) for adults, and 91.6% of pregnancies resulted in recruitment at 8 months. Annual survival rates of adult females averaged 0.96 (95% CI = 0.94–0.98) with hunting included and 0.99 (95% CI = 0.97–0.99) with hunting excluded from calculations. Our fitted model explained 99.8% of past variation in population estimates and represents a useful new tool for short-term management planning. Although we found no evidence of temporal variation in vital rates, variation in population composition caused substantial variation in projected rates of increase ($\lambda = 1.20$–1.36). Restoring documented hunter harvests and removals of elk by the National Park Service led to a potential rate of $\lambda = 1.26$. Greater rates of increase substantiated elsewhere were within the expected range of chance variation, given our model and estimates of vital rates. Rates of increase realized by small elk populations are too variable to support inferences about habitat quality or density dependence. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1141–1148; 2007)

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KEY WORDS *Cervus elaphus*, elk, introduced populations, North Dakota, population dynamics, rate of increase, reproduction, survival, Theodore Roosevelt National Park.

Elk (*Cervus elaphus*) were abundant in the Badlands of North Dakota, USA (Badlands), prior to 1850 (Audubon 1843 in Audubon 1986) but declined during the 1880s (Roosevelt 1888) and were extirpated by 1900 (Bailey 1926). Elk that currently inhabit the southern Badlands are descendants of 47 animals translocated from Wind Cave National Park, South Dakota, USA, to the South Unit of Theodore Roosevelt National Park (THRO) in 1985.

Range expansions and reintroductions provide rare opportunities for the study of ungulate populations that are not subject to resource limitation (Caughley and Birch 1971). Such studies can provide insights about maximum sustainable rates of increase, which are essential for efficient management of large-mammal populations (Eberhardt et al. 1996). These considerations motivate long-standing interest in the dynamics of newly established elk populations (Murphy 1963, Gogan and Barrett 1987, McCorquodale et al. 1988, Howell et al. 2002, Larkin et al. 2003).

Few complications of mathematics, logic, or terminology are involved in understanding population behavior when good estimates of birth and death rates, age and sex composition, and numerical abundance are available; considerable difficulties of interpretation arise when they are not (Eberhardt 1971). Unfortunately, logistic constraints have heretofore prevented the collection of sufficiently detailed information for any newly established elk population. Complexities of population dynamics cannot be understood unless they are studied in terms of relations between the population processes of survival and reproduction (Caughley 1978). Accurate estimates of vital rates are thus a prerequisite for informed planning, evaluation, and modeling of population management strategies (White and Bartmann 1998, Ballard et al. 2000).

To understand relations between population processes and rates of increase, we estimated elk numbers, pregnancy rates, survival rates, age ratios, and sex ratios for reintroduced elk at THRO. We combined rates of survival and reproduction in a population projection model; compared model projections with estimated elk numbers, age ratios, and sex ratios; and generated stochastic projections of population growth for newly established elk populations at Tyson Park, Missouri, USA (Murphy 1963), Afognak Island, Alaska, USA (Burris and McKnight 1973), and the Hanford Site in Washington, USA (McCorquodale et al. 1988, Eberhardt et al. 1996). Our results 1) document rates of survival and reproduction that are among the highest reported for an elk population, 2) provide a context for the interpretation of vital rates and rates of increase that have been reported for newly established elk populations, and 3) provide critical support for elk population management at THRO.

STUDY AREA

The South Unit of THRO encompassed 18,756 ha of unglaciated badlands topography (Laird 1950) near Medora, North Dakota, and was surrounded by the Little Missouri National Grassland and intermingled private lands (Fig. 1). Most of the area was mixed-grass prairie dominated by needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), threadleaf sedge (*Carex filifolia*), and various forbs; however, dense stands of juniper (*Juniperus scopulorum*) occupied some north-facing slopes, and stringers of green ash (*Fraxinus pennsylvanicus*) were associated with draws and watercourses. Stands of cottonwood (*Populus*

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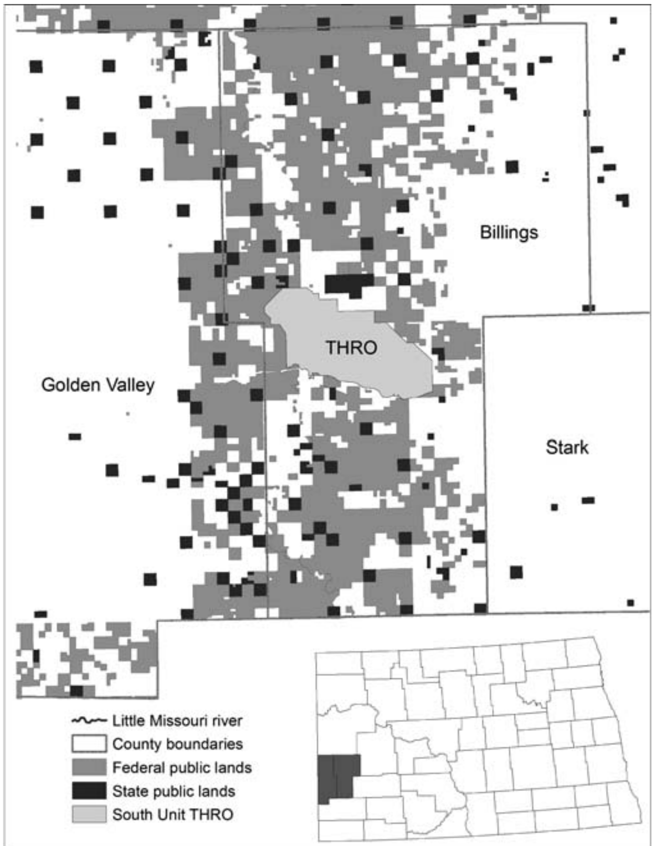

Figure 1. South Unit of Theodore Roosevelt National Park (THRO), North Dakota, USA, where elk were introduced in 1985.

deltoides) occurred along the Little Missouri River (Hanson et al. 1984).

Within THRO, prominent herbivores included feral horses (*Equus caballus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), and black-tailed prairie dogs (*Cynomys ludovicianus*) as well as elk. Horses and bison were confined to the park by a 1.8-m to 2.4-m woven-wire boundary fence. However, >59% of 70 female elk marked with Global Positioning System (GPS) collars during 2003–2004 traversed the park boundary and 11% were migrants that resided primarily outside the park during May through October. Migrants invariably returned by November (G. A. Sargeant, United States Geological Survey, and M. W. Oehler, National Park Service [NPS], unpublished data) and few elk were observed outside the park during winter.

Recreation (e.g., hiking, camping, horseback riding) and park management actions (e.g., weed control, prescribed burning) dominated human activity within THRO. Dominant land uses outside the park included livestock ranching, oil extraction, and agriculture. Elk were hunted outside the park (Oct 1993–1996 and Aug 1997–2005) and were not habituated to human activity. Potential predators of elk included coyotes (*Canis latrans*) and mountain lions (*Felis concolor*).

METHODS

Population Estimates

Our study population originated in March of 1985, when 47 elk were translocated from Wind Cave National Park in South Dakota. That population reportedly included 3 juveniles (<1 yr old; 2 F and 1 M), 3 subadult females (1–2 yr old), 33 adult females (>2 yr old), and 8 subadult males (NPS, unpublished data); however, age classifications were likely incorrect for subadult and adult females.

During 1985–1993, most of the newly reintroduced elk gathered seasonally near the reintroduction site, where they were counted by Sullivan et al. (1988), Westfall et al. (1989), or NPS staff (population totals only; NPS, unpublished data). Our analysis included those counts, which represented minimum population sizes, as well as results of line transect surveys conducted with a Cessna 172 airplane in 2001 and 2004. We used 66 sighting trials with marked groups of elk to estimate detection rates, conditional on group size, and used detection rates to adjusted resulting counts (G. A. Sargeant, unpublished data; M. W. Oehler, unpublished data).

Capture and Classification

We collected data from elk captured by 2 methods. During 1993 and 2000, the NPS reduced elk numbers by using helicopters to herd entire social groups into an ungulate handling facility for translocation. Those groups included representative samples of females and juveniles. After 2000, the NPS retained contractors (Hawkins and Powers Aviation, Greybull, WY; Leading Edge Aviation, Clarkston, WA) to capture individual elk with a helicopter and net-gun, selectively targeting adult females and subadult males.

In 1985 and 1993, NPS personnel used physical and dental characteristics to estimate ages of captured elk. However, it was clear from notes accompanying capture records that 20-month-old subadults were often described as "<3 years old." We reclassified such females as subadults and checked for errors by comparing the population composition and class-specific pregnancy rates with other observed and projected values. We did not reclassify males or elk released in 1985 because 1) our results for males did not distinguish subadults from adults, and 2) elk released in 1985 entered our analysis as adults in 1987. We used patterns of tooth eruption (Hudson and Haigh 2002) to classify elk captured in 2000 or later as juveniles, subadults, and adults. During 2003 and 2004, we extracted a canine tooth from each captured adult elk and used cementum annuli to estimate actual ages (Matson's Laboratory, Milltown, MT). Research protocols (Terrestrials 1.1 and 1.3) were approved by the Research Advisory Committee and Animal Care and Use Committee at Northern Prairie Wildlife Research Center.

Adult and Subadult Survival Rates

During 2000–2001, we marked 47 adult female and 24 subadult male elk with very-high frequency (VHF) radiotelemetry collars for a study of elk movements and distribution. We obtained survival records for January

2000 through August 2001 from R. A. Sweitzer, University of North Dakota. During September 2002 through May 2006, we monitored surviving elk from that study and 104 additional females marked with GPS collars that included VHF telemetry beacons, mortality sensors, and remotely triggered remote release mechanisms (Advanced Telemetry Systems, Isanti, MN). We checked survival with sufficient frequency to determine the month of death and retrieved GPS collars after approximately 10 months of deployment.

We used the Kaplan–Meier method for interval-censored data, with months as intervals, to compute survival rates. When we computed cause-specific rates, we removed elk that died from competing risks from the risk set at the end of the month prior to death. We used the R language and environment (version 2.3.0; R Development Core Team 2005) for statistical analyses and population projections.

Recruitment

We obtained blood samples by venipuncture from female elk captured in 1993, 2000, 2001, and 2003–2006, then tested for pregnancy-specific protein B (Noyes et al. 1997; Bio Tracking, Moscow, ID). We pooled results across years after using Fisher's exact test to compare age classifications, subadult pregnancy rates, and adult pregnancy rates among years of capture. We estimated the population pregnancy rate (p) as a weighted average of subadult and adult pregnancy rates, using class proportions observed in 1993 and 2000 as weights.

Juvenile survival rates (s_j) typically have been estimated from numbers of juveniles (n_j), numbers of subadult and adult females (n_f), and pregnancy rates ($s_j = n_j/[p \times n_f]$; e.g., Flook 1970, Merrill 1987, Coughenour and Singer 1996). We computed a similar estimate for comparison. However, unadjusted rates are likely to overestimate actual survival rates if juveniles can survive deaths of their mothers. At THRO, juveniles may well have survived in most cases because adult mortalities predominantly occurred after juveniles reached 2 months of age, when rumen function was fully developed (Cook 2002). Consequently, we also used a more conservative estimator that incorporated adult survival rates (s_{ad}) to inflate n_f and adjust for maternal losses ($s_j = [n_j \times s_{ad}]/[p \times n_f]$).

Population Projections

Model structure.—We used estimates of vital rates to parameterize a deterministic population model that described population growth from 1987 through 2005. We excluded 1985 and 1986 because demographics of the newly reintroduced elk reflected conditions at Wind Cave National Park and stresses associated with translocation. By using our model to consider projected and observed elk numbers, age ratios, and sex ratios in a coordinated fashion, we were able to strengthen individual parameter estimates, reconstruct growth of the population, and estimate potential rates of increase.

The life-cycle graph (Caswell 1989, Ebert 1999) shown in Fig. 2 described our model. In Fig. 2, nodes (circles) represent states an elk could occupy at midwinter (approx. Jan). Transitions among nodes occurred at rates denoted by parameters that represented rates of survival and reproduction. Because numbers of elk killed by hunters and numbers of elk removed by the NPS were not proportional to elk abundance, we subtracted documented removals and did not include such losses when computing survival rates. Solid lines represented transfers of individuals between states and dashed lines represented reproductive contributions to states.

Model parameters included survival rates of females >20 months of age (s_f), proportions of January pregnancies that produced 8-month-old juveniles the following year (s_0), survival rates of males >20 months of age (s_m), and pregnancy rates of subadult (p_{sub}) and adult (p_{ad}) females. We used s_f to approximate survival rates for elk 8–20 months of age because we could not compute separate parameter estimates for this age class. Based on sex ratios of juveniles captured in 1993 and 2000, we assigned a sex ratio of 1:1 at 8 months of age.

When population growth is described as a discrete process occurring in a series of annual steps, as typically is the case for elk, the result is a geometric series. For a geometric series, the rate of increase is described by a population multiplier, λ, or by R, where t is an integer and $\lambda_t = N_{t+1}/N_t = 1 + R_t$. When population growth is a continuous exponential process, the rate of increase is described by $r = dN/dt$, and $N_t = N_0 e^{rt}$ for $t > 0$. In practice, these concepts and notation often are mixed. For consistency, we described increases in terms of λ or as percentages ($100 \times R$), transforming previously published results where necessary.

Model fitting.—Estimating model parameters directly from field observations is inefficient (i.e., wasteful of information) when related estimates of abundance and population composition are available. We thus used weighted least squares (White and Lubow 2002) to estimate model parameters from multiple sources of information that included age ratios, sex ratios, and elk numbers as well as our estimates of vital rates.

We used the solver package in Microsoft Office Excel 2003 (Microsoft Corporation, Redmond, WA) for model fitting. During fitting, we used direct estimates as initial values and associated standard errors, when available, to rescale residuals. However, standard errors were not estimable for most observations of age ratios, sex ratios, and elk numbers, so we assigned a coefficient of variation ($SE/\bar{x}$) of 0.05. In general, larger coefficients of variation improved the correspondence between field estimates and fitted model parameters, whereas smaller values produced closer fits to age ratios, sex ratios, and elk numbers. We chose 0.05 because fitted values for model parameters were not sensitive to the value chosen for coefficients of variation >0.03 to 0.05.

Population projections.—We estimated the potential rate of increase (Caughley 1978) for THRO by restoring elk to projections if they were harvested by hunters or removed by the NPS. To gain insights about relations between vital rates and observed rates of increase, and to place our results in

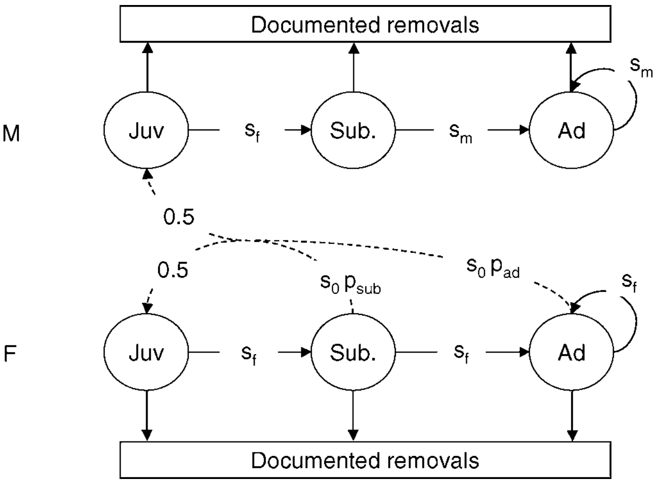

Figure 2. Schematic depiction of a population model used to describe growth of an introduced elk population at Theodore Roosevelt National Park, North Dakota, USA, 1987–2004. Sub. = subadults.

context with previous reports, we used random draws from binomial distributions to incorporate variation in primary sex ratios, numbers of births, and numbers of mortalities that occurred each year. We used this stochastic implementation of our model to project growth in numbers of female elk for populations of variable size and composition. We also used our model to project growth of elk populations on Afognak Island, Alaska, from 1930 to 1937 (Burris and McKnight 1973, Gogan 1986); at Tyson Park, Missouri, from 1951 to 1959 (Murphy 1963); and at the Hanford Site in Washington from 1983 to 1993 (McCorquodale et al. 1988, Eberhardt et al. 1996). For the Hanford projection, we subtracted annual removals documented by Tiller et al. (2000). We selected those populations as examples for further study because the initial population composition and an exceptional rate of increase were reported in each case.

RESULTS

Population Growth

Elk numbers increased from 47 in March of 1985 to approximately 350 by January of 1993 (Fig. 3). In January of 1993, the NPS captured 280 elk, including 52 juvenile females, 35 juvenile males, 47 subadult females, 30 subadult males, 110 adult females, and 6 adult males. Of these, 221 animals (43 juv F, 35 juv M, 39 subad F, 30 subad M, 69 ad M, and 5 ad M) were removed from the population, reducing elk numbers to approximately 130. Numbers subsequently increased to >410 in January of 2000, when the NPS captured 297 additional elk (45 juv F, 45 juv M, 50 subad F, 34 subad M, 122 ad F, and 1 ad M) and removed 203 (36 juv F, 39 juv M, 25 subad F, 13 subad M, 89 ad F, and 1 ad M), reducing the population to >198. Aerial surveys resulted in midwinter population estimates of 304 in 2001 and 528 in 2004 (Fig. 3). During 1997–2005, documented hunter harvests included 338 elk (8 juv, 74 subad and ad F, and 256 subad and ad M) from hunting units adjacent to the park.

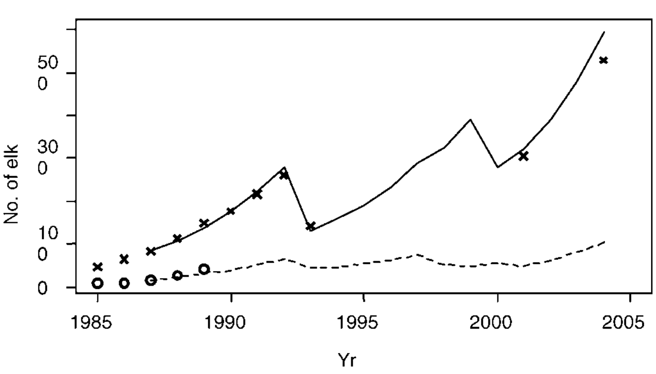

Figure 3. Comparisons of winter counts (× = all elk, ○ = subad and ad M) and fitted model projections for a reintroduced elk population at Theodore Roosevelt National Park, North Dakota, USA, 1985–2004.

Age and Sex Ratios

Age ratios (juv:subad F:ad F) of antlerless elk were similar in 1993 and 2000 ($P \approx 0.94$, $n = 506$). Antlerless elk were 35% juveniles (SE ≈ 2.1%), 19% subadults (SE ≈ 1.7%), and 46.0% adult females (SE ≈ 2.2%). These proportions equate to 0.54 juveniles per potentially reproductive female (SE ≈ 0.052) and 0.76 juveniles per adult female (SE ≈ 0.077). P-values and standard errors are approximate because juveniles, subadults, and adults do not occur in groups independently.

The difference between sex ratios of juveniles in 1993 (59.8% F, SE = 5.3%, $n = 87$) and 2000 (50.0% F, SE = 5.3%, $n = 90$) was not greater than expected due to chance ($P = 0.23$). Pooling the data resulted in an estimated sex ratio of 1.2 females:male (54.8% F, SE = 3.75%, $n = 177$). The chance of observing such a deviation, given a 1:1 population sex ratio and a sample of $n = 177$, was 0.47.

Adult Survival

We monitored the survival of 184 females for 3,710 elk-months and 24 males for 476 elk-months (1 elk for 1 month = 1 elk-month). Eight females were killed outside THRO by hunters and 3 were found dead within the park. Carcasses of females that died within THRO were intact when found and proximate causes of death were not evident. We lost radio contact with 2 females and counted them as losses to unknown causes. Annual survival rates of females averaged 0.96 (95% CI = 0.94–0.98) with hunting included and 0.99 (CI = 0.97–0.99) with hunting excluded from calculations.

Eleven males were killed outside THRO by hunters, 6 died of unknown causes outside the park, and 2 were found dead of unknown causes within the park. One male dispersed (collar recovered near Handel, Saskatchewan, Canada [52.0668°N, 108.722°W], 684 km from THRO), one was dispatched by the NPS after becoming trapped in a sinkhole, and one died after becoming entangled in the park boundary fence. We lost radio contact with 2 males and counted them as losses due to unknown causes. Annual survival rates of males averaged 0.52 (CI = 0.40–0.68) with hunting and emigration included among losses, and 0.68 (CI = 0.54–0.84) with hunting excluded from calculations. The maximum age attained by a marked male was 6 years (n

= 2 elk). Others were lost at ages of 2 ($n = 12$), 3 ($n = 4$), 4 ($n = 4$), and 5 ($n = 2$) years.

Recruitment

We tested 373 elk of known age class, including 162 elk of known age, for pregnancy. We found no evidence of an association between year of capture and subadult ($P = 0.79$) or adult ($P = 0.50$) pregnancy rates. Class pregnancy rates averaged 54.1% (SE = 5.4%, $n = 85$) for subadults and 91.0% (SE = 1.7%, $n = 288$) for adults. Ninety of 93 adults 2–12 years of age were pregnant (96.8%, SE = 1.8%): in contrast, only 1 of 5 adults $\geq$13 years of age was pregnant. Nonpregnant adults of known age were 4, 5, $\geq$13, 14, 15, and $\geq$17 (2 elk) years of age. When weighted by class proportions observed in 1993 and 2000, these results led to an estimated population pregnancy rate of 80.1% (SE = 2.0%). Pregnancy rates, female survival rates, and age ratios of elk captured in January indicate that 91.6% (adjusted estimate) to 95.2% (unadjusted estimate) of pregnancies observed in January produced a juvenile that survived to 8 months of age.

Population Projections

Fitted model parameters differed only slightly from field estimates supplied as initial values: s_f decreased from 0.986 to 0.964, s_0 increased from 0.910 to 0.924, s_m decreased from 0.675 to 0.661, p_{sub} increased from 0.541 to 0.579, and p_{ad} was essentially unchanged (0.908). Fitted numbers of juveniles per potentially reproductive female ($\bar{x} = 0.61$) were similar to observed ratios ($\bar{x} = 0.57$), as were proportions of antlered males (fitted $\bar{x} = 20\%$; estimated $\bar{x} = 22\%$), and the fitted model explained 99.8% of past variation in population estimates (Fig. 3).

Although we used a deterministic model to describe population growth, rates of increase varied substantially (Fig. 3). Variation was due in part to removals by hunters and the NPS and in part to changes in herd composition that resulted from selective removals of females and subadults by the NPS (Jan 1993 and 2000) and selective removals of males by hunters (Aug 1997–2005). Projected rates of increase based on winter herd composition (Fig. 4) ranged from 1.20 in 1994 to 1.36 in 1985. Restoring documented removals by the NPS and legal hunting to model projections resulted in a potential rate of $\lambda = 1.26$ and a midwinter population consisting of 61 juveniles and 49 antlered males/100 females $\geq$20 months of age.

Elk numbers at Tyson Park, Missouri, increased from 10 in 1951 to 103 in 1959 ($\lambda = 1.34$), when the population included 24 juveniles (23%), 11 subadult males (11%), 51 subadult and adult females (50%), and 17 adult males (16%; Murphy 1963). For 1959, our model predicted an average population size of 89 (95% prediction CI [PI] = 76–123; $\lambda = 1.32$; Fig. 5), including 26 juveniles ($\bar{x} = 29\%$; PI = 24–33%), 42 subadult and adult females ($\bar{x} = 48\%$; PI = 41–54%), 10 subadult males ($\bar{x} = 11\%$; PI = 6–17%), and 11 adult males ($\bar{x} = 12\%$; PI = 6–20%).

Projected rates of increase and population sizes were similar to estimates for the Hanford Site (Fig. 5). Estimated

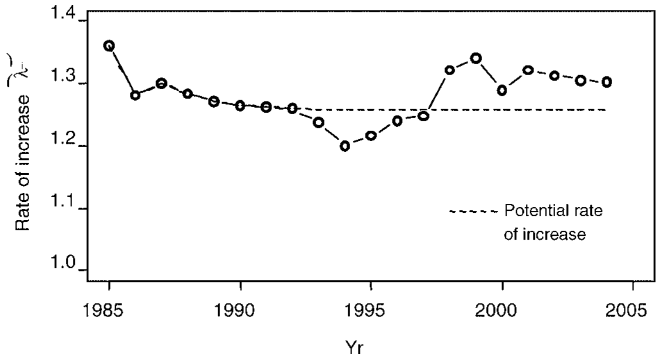

Figure 4. Rates of increase projected from the January composition of a reintroduced elk population at Theodore Roosevelt National Park, North Dakota, USA, 1985–2004.

and projected population composition were comparable only during the initial period (1983–1986) of rapid population growth: during that period, the estimated composition of the population was 24% juvenile, 41% subadult or adult female, 13% subadult male, and 22% adult male. Projected composition was 27% juvenile (PI = 25–30%), 42% subadult or adult female (PI = 40–45%), 13% subadult male (PI = 12–14%), and 17% adult male (PI = 14–20%).

Population sizes reported for elk on Afognak Island, Alaska, during the 1930s were likely incorrect. They exceeded the 95th percentile of projected numbers (Fig. 6) even when we specified unprecedented vital rates (subad and ad survival = 1, ad pregnancy = 1, subad pregnancy = 0.75; 95% of pregnancies recruited).

DISCUSSION

Vital Rates

For most long-lived species, rates of increase are especially sensitive to changes in adult female survival; however, survival rates of adult females typically exhibit a comparatively narrow range of natural variation (Eberhardt 2002). Variation in adult female survival can thus have profound management implications and yet be difficult to detect (Nelson and Peek 1982). The observed rate of mortality for female elk at THRO was nevertheless measurably lower than for some unhunted populations (cf. Ballard et al. 2000, Garrott et al. 2003). Low mortality was consistent with a very high observed rate of increase, nonselective removals by the NPS, and minimal hunter harvest. All of these factors contributed to a population that consisted predominantly of young animals with very low risks of mortality.

Precise estimates of loss rates for males were a lower priority than precise estimates of female survival because losses of males primarily affect sex ratios. We also anticipated some bias because adult males were marked at 20 months of age (a consequence of group composition in 2000). We expected the population to include 2 groups with different survival probabilities: young males that were likely to traverse the park boundary and experience high mortality rates, and resident older males that did not engage in such high-risk behavior. In retrospect, however, relatively short life spans of males were strong support for low recruitment

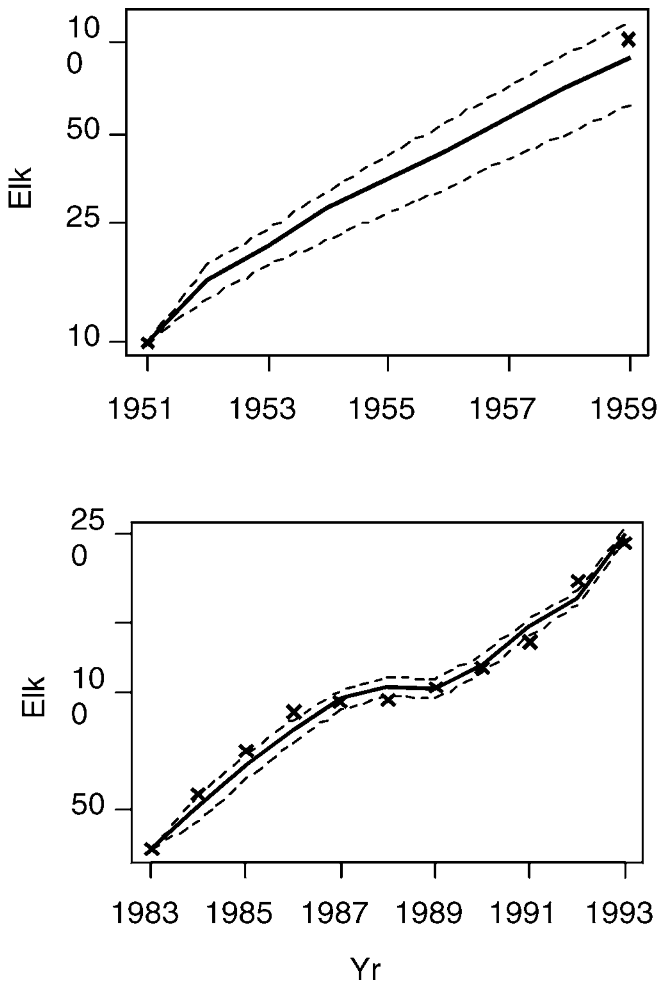

Figure 5. Comparisons of observed (×) and projected elk numbers for Tyson Park, Missouri (top; Murphy 1963) and Hanford, Washington, USA (bottom; McCorquodale et al. 1988, Eberhardt et al. 1996). Dashed lines delimit 95% prediction confidence intervals for projected population sizes.

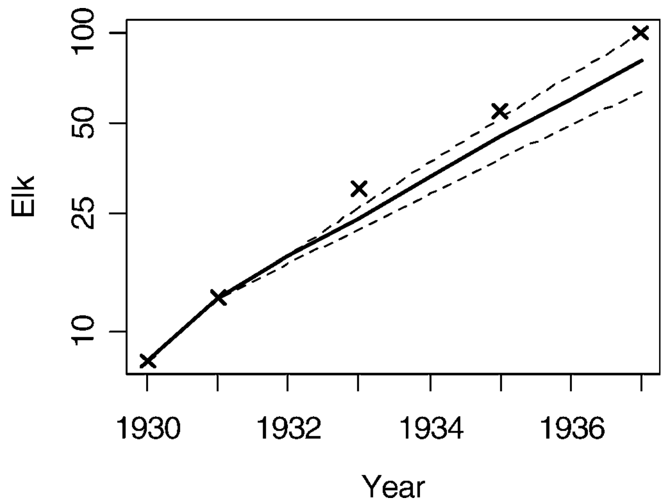

Figure 6. Comparison of model projections with population sizes reported for elk on Afognak Island, Alaska, USA (×; Burris and McKnight 1973). Reported population sizes exceed 95% prediction confidence limits for projections based on unprecedented vital rates (pregnancy rates of 75% for subad and 100% for ad, recruitment of 95% of pregnancies, and 100% survival of recruits).

of older males. Substantially lower loss rates would also have been inconsistent with observed sex ratios.

Subadult pregnancy rates and juvenile survival rates are relatively sensitive indicators of population status for long-lived vertebrates in general (Eberhardt 2002) and elk in particular (Houston 1982, Coughenour and Singer 1996). At THRO, we effectively ruled out subadult pregnancy rates <45% (95% lower bound). We have not encountered conclusive published evidence of higher subadult pregnancy rates. When higher rates have been observed, they typically have been associated with small samples and may have occurred by chance (e.g., 83%, $n = 6$, Eberhardt et al. 1996; 75%, $n = 4$, McCullough 1969; 69%, $n = 13$, Houston 1982).

Age ratios observed in January were similar to those reported by McCorquodale et al. (1988) for elk at the Hanford Site and by Bender et al. (2002) in Michigan, USA, and reflected exceptionally high rates of survival to 8 months of age. Given very high survival rates to 8 months of age, typically mild winter weather, abundant forage, and the fact that instances of winterkill and predation have never been documented at THRO, juvenile survival rates from 8 months to 1 year of age likely were similar to adult survival rates.

Some theoretical arguments (Trivers and Willard 1973) and empirical evidence (Smith et al. 1996, Kohlmann 1999) have suggested a link between maternal condition and fetal sex ratios of elk, such that females in good condition may be expected to produce preponderantly male offspring (but see Clutton-Brock et al. 1981, Thomas et al. 1989). If fetal sex ratios differed from unity at THRO, the departure was no longer detectable by 8 months of age. When they occur, gender-related differences in survival rates of juvenile elk are expected to favor females (Clutton-Brock et al. 1985, Smith and Anderson 1998). However, very low mortality rates limited the potential for differential survival of male and female juveniles at THRO.

Population Growth

In principle, dynamics of newly established populations are thought to provide insights about maximum rates of increase that can be achieved when animals are released from resource limitation (Caughley and Birch 1971). These intrinsic rates of increase are expected to vary as a result of environmental influences (Caughley and Birch 1971, Caughley 1978) and have long been considered the appropriate statistic for comparing the favorability of 2 environments occupied by 1 species (Caughley 1978).

In context with these principles, it seems logical to 1) use rates of increase achieved by newly established populations to estimate intrinsic rates (Raedeke et al. 1986, Gogan and Barrett 1987, McCorquodale et al. 1988, Eberhardt et al. 1996), 2) ascribe spatial variation in observed rates of increase to environmental influences (e.g., Raedeke et al. 1986, Gogan and Barrett 1987), and 3) expect newly established populations to achieve—but not sustain—high initial rates of increase. Declining rates have long been associated with environmental impacts of herbivory and density-dependent competition for resources (Leopold 1943, Banfield 1949, Caughley 1970).

At THRO, a mild environment and abundant forage contributed to exceptionally high rates of recruitment and female survival that persisted for 2 decades. Projected rates of increase nevertheless declined from 1987 to 1994 and, even after adjusting for removals, were among the lowest reported for a newly established elk population. These counterintuitive results reflect changes in population composition and the stochastic nature of underlying birth and death processes. Our simulations showed that the highest rates of increase (34–36% annually; Murphy 1963, Gogan and Barrett 1987, McCorquodale et al. 1988) that have been substantiated for insular elk populations could be explained by population structure and chance variation in birth rates, death rates and sex ratios, given vital rates we observed at THRO. The much greater rate of increase (45% annually) reported for elk on Afognak Island, Alaska, during the 1930s (Gogan 1986, Gogan and Barrett 1987, Raedeke et al. 2002) was likely a consequence of erroneous population estimates. Such errors are always a concern when historic data that do not meet current standards of methodology or documentation are used for purposes other than originally intended.

Population Projections

Rates of increase are affected by environmental variation in vital rates and by chance variation in numbers of births, numbers of deaths, and sex ratios at birth. Survival rates of elk are likely to be greater for prime-aged females than for subadults, and to decline, along with reproductive rates, with advanced age (Caughley 1966, Houston 1982, Loison et al. 1999). Model projections are also subject to uncertainty resulting from the estimation of parameters. Population growth at THRO was nevertheless described with surprising accuracy ($r^2 = 0.998$) by a deterministic model based on 3 age classes and only 5 parameters. These represented female and subadult survival (s_f), adult male survival (s_m), and the recruitment of juveniles at 8 months of age ($s_0 p_{sub}$ and $s_0 p_{ad}$).

We initially devised a simple class-structured model because available data did not support more detailed descriptions of population processes. The resulting fit corresponded well with parameter estimates derived from field data, observed counts, and observed age ratios, thus ruling out a need for more complicated structure. In retrospect, model fit was a logical consequence of the relatively mild climate and abundant forage that characterized THRO. Necessary approximations (e.g., a common survival rate for subad and ad F) were reasonable because vital rates were essentially constant and near biological maxima. For example, we could not document a single instance of predation or winterkill, the principle proximate causes of age-related and environmental variation in survival rates of elk.

A class-structured model was satisfactory because 1) vital rates are relatively consistent for prime-aged ungulates (Loison et al. 1999), including elk (White et al. 2003, Cook et al. 2004); and 2) high recruitment rates resulted in an adult class that consisted predominantly of prime-aged elk. Class averages were thus robust to effects of senescence and variation in population composition. Agreement between projected and observed numbers and composition for several populations provides added assurance that model projections were robust to typical variation in the vital rates and structure of rapidly increasing elk populations.

MANAGEMENT IMPLICATIONS

Our results emphasize the need for managers to interpret vital rates and rates of increase as stochastic processes, in context with population size and composition, when predicting or interpreting the dynamics of small elk populations. Our relatively simple model accurately described the growth and composition of several rapidly increasing herds and can be used to facilitate such investigations. Our model and parameter estimates are also likely to be useful for management planning at THRO; however, long-term model projections are sensitive to compounding effects of small changes in parameters. Consequently, the close fit of our projections to historical counts, age ratios, and sex ratios does not imply an ability to make equally accurate long-term predictions. Model projections will be most useful for comparing hypothetical management strategies, smoothing series of population estimates, and short-term (approx. 2–4 yr) management planning. If elk densities continue increasing beyond historic limits, vital rates should be monitored to assure the continued relevance of parameter estimates.

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